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RECONSIDERATION OF THE EVIDENCE FOR A COMMON DINOSAUR-AVIAN STEM IN THE PERMIAN.

DINOSAUR CONTRIBUTIONS, NO. 4.[1]

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THE relation of dinosaurs to birds has been one of the most attractive problems of comparative anatomy during the thirty-seven years which have elapsed since Gegenbaur's observation that the tibiotarsus of Compsognathus, one of the smallest carnivorous dinosaurs, closely resembles that of the bird.

Since a number of new avian resemblances have recently been discovered among dinosaurs, it seems important to reconsider this much debated problem.

I. AVIAN RESEMBLANCES IN CARNIVOROUS BIPEDAL DINOSAURS.

We owe to Fürbringer (**'88**, p. 1592) a valuable historical summary of the literature and progress of opinion. The recognition of avian characters among dinosaurs has been generally

[1] Presented before the American Association for the Advancement of Science, Section Zoölogy, June 27, 1900.

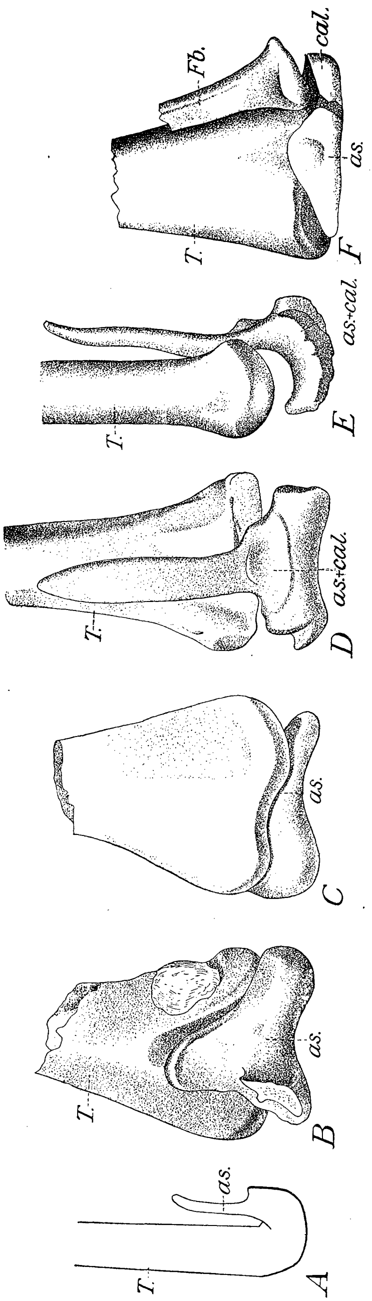


FIG. 1. — Ankle joint of dinosaurs and birds, tibiotarsus. *A*, pigeon (Columba), after Baur; *B*, carnivorous dinosaur (Megalosaurus), after Cuvier; *C*, the same, back view; *D*, young ostrich (Struthio), after Baur; *E*, the same, from the side; *F*, Ornithotarsus, from Baur, after Cope.

attributed to Cope and Huxley; but it appears that Gegenbaur enjoys the priority; for, in 1864 (**'64**), he pointed out that Compsognathus in the structure of its tarsus presents a transition stage between birds and reptiles, or a species of double relationship, which in fact pervades the entire skeleton. Cope (**'66**, p. 317; **'67**, pp. 234, 235; **'69**, p. 123) made a similar observation in Lælaps, the great carnivorous Upper Cretaceous dinosaur, and considered the carnivorous dinosaurs in general as intermediate in position between reptiles and birds, adding to the list of avian characters the elongation of the vertebræ of the neck and the very light construction of the arches of the skull.

Unaware of Cope's observations, Huxley's attention was directed to the matter by Professor Phillips's collection of carnivorous dinosaur (Megalosaurus) remains in the Oxford Museum; fresh from his memoir on the classification of birds, published in 1867, his eye was

keen for avian resemblances, and he at once noted that the ilium of Megalosaurus was bird-like. In fact, Phillips had previously noted the resemblance of this bone to that of Apteryx.

Stimulated to further comparison, Huxley ('69, pp. 15 f.) observed other avian features, *viz.*, that the ischium of dinosaurs extends back parallel with the ilium; that the pre-acetabular process, or pubic peduncle of the ilium, extends further downward than the post-acetabular, or ischial peduncle; that the acetabulum itself is partly open; that the limb bones are distinctly tubular; that the scapulo-coracoid elements are anchylosed together; that the sacrum is partly ornithic, partly reptilian; that the femur is vertical to the body, its head extending outward into the acetabulum; that the tibia possesses a prominent procnemial crest; that the astragalus embraces the lower end of the tibia. Huxley concluded ('68) "there could be no doubt that the hind quarters of Dinosauria wonderfully approached

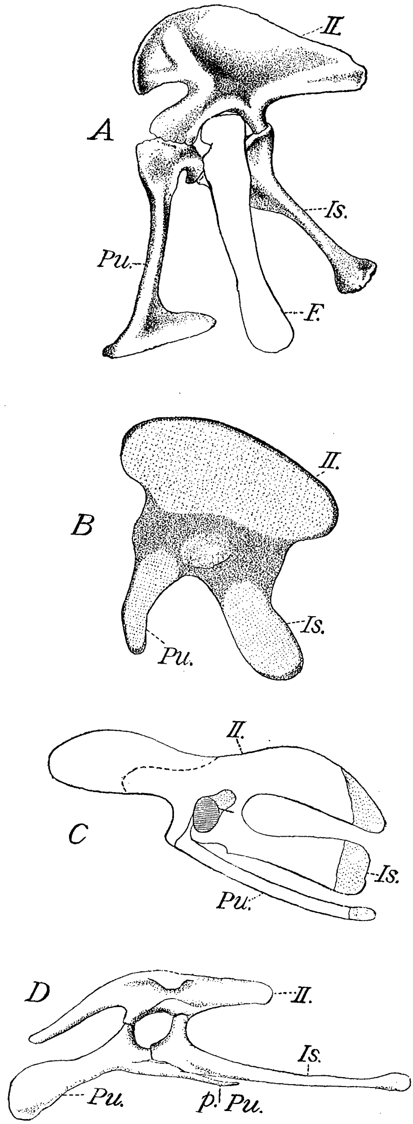


FIG. 2. — Pelvic arch of left side, dinosaurs and birds. *A*, carnivorous dinosaur (Allosaurus), triradiate type, after Marsh; *B*, embryonic bird (Larus), triradiate type, after Mehnert; *C*, adult bird, pubis rotated backwards, after Gegenbaur; *D*, iguanodont dinosaur, vestigial postpubis, quadri-radiate type, after Marsh.

those of birds in their general structure, and, therefore, that these extinct reptiles were more closely allied to birds than any which now lived." He did not commit himself to the theory of direct ancestry, however, as shown in the following passage: "It may be regarded as certain that we have no knowledge of the animals which linked reptiles and birds genetically, and that the Dinosauria, with Compsognathus, Archæopteryx, and the struthious birds only help us to form a reasonable conception of what these intermediate forms may have been." In one important anatomical point Huxley was in error, since he believed that the pubis of dinosaurs, like that of birds, was directed backwards; whereas we now know that in all dinosaurs the pubis is directed forwards, like that of other reptiles. Huxley's ideas culminated in his proposal of the group Ornithoscelida, or "bird-limbed" reptiles, to embrace two suborders, Dinosauria and Compsognatha. The latest expression of Huxley's opinion is found in his paper on the "Respiratory Organs of Apteryx" ('**82**, p. 569): "Thus, notwithstanding all the points of difference, there is a fundamental resemblance between the respiratory organs of birds and those of crocodiles *pointing to some common form (doubtless exemplified by some of the extinct Dinosauria), of which both are modifications.*" (The italics are our own.) Huxley's final view, therefore, was that birds sprang from some primitive and unknown type of dinosaur.

The conception of direct descent of birds from dinosaurs gained ground until it reached the force of positive theory in the writings of Hoernes, and especially of Marsh, as seen in the following paragraph ('**77**, p. 228): "It is now generally admitted by biologists who have made a study of the vertebrates that birds have come down to us through the dinosaurs, and the close affinity of the latter with recent struthious birds will hardly be questioned." Subsequently, however, Marsh ('**80**, p. 188) pointed out that the absence of feathers in dinosaurs and pterosaurs and the presence of a free quadrate in birds rendered it probable that birds descended not from dinosaurs but from a more ancient sauropsid form.

II. Rise of the Theory of Homoplasy.

The theory of direct descent was more or less strongly supported by many anatomists, but there were also many dissenters. Seeley (Fürbringer, '**88**, p. 1595) pointed out with truth that the direct descent theory rested upon resemblances of certain bones of the pelvis and posterior extremities which are found only in certain genera and are not characteristic of the whole group.

Vogt also advocated the homoplastic view. Their opinions ('**79**) were given by Seeley ('**81**) as follows :

"'All the characters whereon are based the claim of dinosaurs to be regarded as the ancestors of birds are only related to the power of keeping an upright position upon the hind feet.'

"Vogt believes that certain dinosaurs were leaping or perching animals, and infers that the avian characters of the pelvis and hind limbs thus came to be evolved from community of habit with birds. He is, however, not indisposed to see in dinosaurs possible parents of the ratites; while the Archæopteryx would be the ancestor of the birds that fly."

In 1882 Dollo also ('**82**, '**83**) advanced the more modern idea that the resemblances in the pelvis and hind limbs might as well be considered adaptive as genetic. Baur, however ('**83**, pp. 417 f.; '**85** (2), pp. 446 f.), held firmly to the idea of direct descent, singularly enough, not through the carnivorous dinosaurs, but through the herbivorous iguanodont types. Dames, in opposition to Baur ('**84**), concluded with Vogt, Seeley, and Dollo that the resemblances were due to adaptation, and that the direct ancestors of the birds could not be designated. A still more conservative view, that the resemblances were altogether due to adaptation and not at all indicative of genetic descent, was taken by Richard Owen, by W. K. Parker ('**87**), by Cleland ('**87**), and by Mehnert ('**88**). In the mean time, however, Owen, Cope, Mivart, Wiedersheim, had more or less strongly advocated the theory of the derivation of the carinate birds from the pterosaurs. Thus arose the extreme theory of Mivart ('**81**) that the carinate birds sprang from pterosaurs,

and the ratite birds from dinosaurs. This was supported by Wiedersheim (**'86**).

As a result of his own detailed review and comparison, Fürbringer in his great monograph upon birds (**'88**, p. 1624) concludes that the direct descent of birds from any known type of Dinosauria is excluded; that the birds are monophyletic; that the resemblances between dinosaurs and birds are all "convergence-analogies" and "parallels" due to relationship of the "middle grade"; more definitely (**'88**, p. 1630), he regards Dinosauria, Crocodilia, and Lacertilia in the order named as the nearest relatives of birds, and believes that the stem of the birds is to be sought in a common sauropsidan ancestor lying between the Dinosauria, the Crocodilia, and the Lacertilia; that this stem, as Marsh had already supposed, is to be found in the last division of the Palæozoic, namely, the Permian; here occurred the first differentiation of fine sauropsidan scales into feathers.

The problem thus presents itself now in three forms: (1) are birds directly descended from primitive dinosaurs? (2) have birds and dinosaurs originated from a common stock? (3) are the remarkable resemblances between these two groups entirely due to parallelism or homoplasy?

Before discussing this triple problem we may continue with the subject of the resemblances and differences, or positive and negative evidence.

III. Additional Avian Resemblances in Bipedal Dinosaurs.

Cervical Vertebral Formula. — Fürbringer (**'88**) observes that the cervical + cervico-dorsal vertebræ of birds vary from ten to eleven (Archæopteryx) to twenty to twenty-five in the larger, long-necked forms, indicating that the number of vertebræ is distinctively an adaptive character. More in detail, we may give the avian formulæ as follows:

VERTEBRAL FORMULÆ OF BIRDS.[1]

	Cervicals (with Co-alesced Ribs).	Cervico-Dorsals (with Ribs not attached to Sternum).	Dorsals (with Ribs partly attached to Sternum).	Total Number of Cervico-Dorsals and Dorsals.	Total Number of Pre-sacrals or Cervicals, Cervico-Dorsals, and Dorsals.	Sacrals (including Pelvic Vertebræ).	Caudals.
Archæopteryx[2]	10, 11	—	—	11 or 12	21 ?	5, 6	20 or 21
Apteryx	16	1, 2	7, 8	8–10	24–26	—	—
Dromæus	20, 21	2–4	5–7	7–11	27–32	—	—
Struthio	20	2, 3	5	7, 8	27, 28	—	—
Hesperornis[3]	17	—	—	—	23	14	12
Anser cinereus	18	2	4	6	24	—	—
Cygnus olor	23	2	4, 5	6, 7	29, 30	—	—
Most Passeres	14	2, 3	5	7, 8	21, 22	—	—

From this table can be drawn the general conclusion, positive or favorable to the common dinosaur-avian stem theory, that primitive birds had numerous cervicals, few dorsals, and numerous caudals.

Pubis of Birds.—An important negative contribution to this problem is that upon the pubis by Mehnert (**'88**), who shows that the pubis of birds in the earliest stages of development is directed forwards, like that of dinosaurs and other reptiles, and is *secondarily* shifted backwards, parallel with the ischium; that the *processus ileopectineus*, rising mainly from the ilium, is a secondary structure, exclusively characteristic of birds, which has no homology with the falsely called prepubis of dinosaurs; thus the various comparisons of the bird and dinosaur pelvis by Huxley and others lose one of their strongest supports. The primitive (or embryonic) bird pelvis, however, is triradiate and resembles that of the primitive carnivorous dinosaurs. The secondary, or adaptive, bird pelvis is totally different from that of any dinosaur. This militates against the theory of the derivation of birds from any specialized dinosaurs, such as the Iguanodontia or Megalosauria, but not against the theory of a common dinosaur-avian stem.

[1] Mainly from Newton, **'93–'96**, p. 849.
[2] Fürbringer, **'88**. [3] Marsh, **'80**.

Musculature of Leg. — Dollo ('83, 2) adds an extremely interesting resemblance in his comparison of the attachment of the muscles connecting the back of the femur with the ischium and with the caudal vertebræ in birds and in Iguanodon; he shows that the so-called "third trochanter" of birds and dinosaurs, to which the name "fourth trochanter" should be

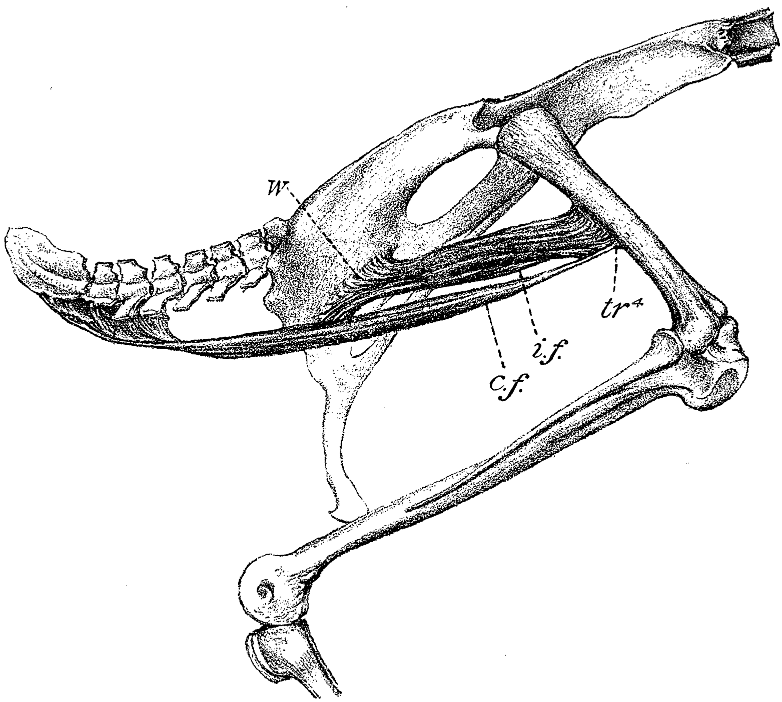


FIG. 3. — Right hind limb of duck (Anas boschas), showing, tr^4, the supposed 4th trochanter; *i.f.*, ischio-femoral; *c.f.*, caudo-femoral muscles. After Dollo.

applied, is actually a process quite distinct from the "third trochanter" of mammals, that its function is especially for the insertion of the "ischio-femoral" muscle and for the origin of the "caudo-femoral" muscle; he concludes that the femur of Iguanodon is constructed upon the bird and not upon the reptilian type, and, as a corollary of this, that the extrinsic musculature of the tail in Iguanodon presented close resemblances to the corresponding musculature in the bird. As

shown in Fig. 3 there are two muscles at the back of the femur, the larger of which, or "ischio-femoral," passes from the crest of the fourth trochanter back to the ischium; while the more slender "caudo-femoral" passes from the apex of the fourth trochanter back to the caudals and causes the sudden lateral movements of the tail, so characteristic of the duck. The pronounced development of this character in Iguanodon indicates a very powerful "caudo-femoral" muscle in this type. Further, Dollo observes that Hesperornis, with its well-developed tail, presents a condition of the fourth trochanter intermediate between the avian and dinosaurian types.

FIG. 4. — Carnivorous dinosaur (Allosaurus), right hind limb, × $\frac{1}{16}$. After Osborn.

Returning to the carnivorous bipedal dinosaurs, Osborn ('99 (2), p. 163) described the complete hand and foot of Megalosaurus from the famous Bone Cabin Quarry. Of greatest interest is the first digit, or hallux, not before described; proximally the metatarsal of this toe (I) persists and fits into a shallow groove of metatarsal II; the

shaft is, however, entirely interrupted in the middle portion; distally it is fitted to the rounder posterior portion of the shaft of metatarsal II, demonstrating that it was directed inward like the small hallux of Apteryx; unlike this bird, however,

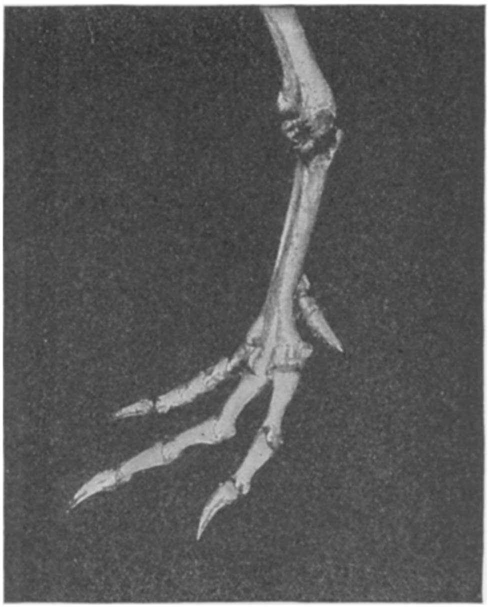


FIG. 5. — Hind foot of bird (Apteryx). Internal view of right tibiotarsus and pes. After Osborn.

Megalosaurus possessed a complete and functional phalanx and claw upon the hallux, which undoubtedly were of service in grasping, as in carnivorous birds.

IV. AVIAN RESEMBLANCES IN QUADRUPEDAL DINOSAURS.

It will be noted that all the resemblances above recorded relate exclusively to the bipedal bird-footed carnivorous and herbivorous dinosaurs, namely, to the Megalosauria and Iguanodontia. The resemblances pointed out below refer to the entirely distinct group of Cetiosauria or Sauropoda, which, in contrast, are quadrupedal and reptile-footed.

In describing Camarasaurus, Osborn ('98, p. 220) directed attention to the resemblance between the cervicals and anterior

"cervico-dorsals" of the Sauropoda and those of the emeu (Dromæus), as follows: "The long neck, similar in structure and almost as flexible as that of an emeu (Dromæus), could thus pass through a prodigious arc in the search for food, either under or above water. The neck motion partly involved the anterior non-spine-bearing dorsals (vertebræ with free ribs, equivalent to the 'cervico-dorsals' of birds), as in Dromæus, behind which the comparatively inflexible, large, spine-bearing dorsals rose to maximum height in the sacrum for the inser-

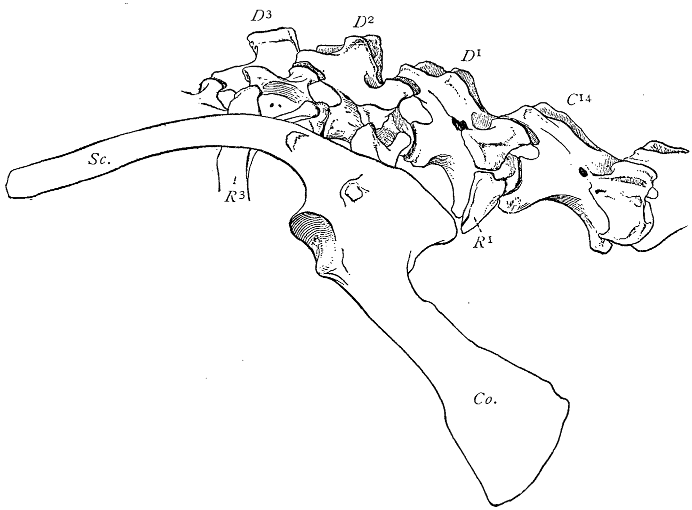


FIG. 6. — Neck of bird (Dromæus). Cervicals 13–14 and cervico-dorsals 1–2 entirely lacking median spines; dorsal 3 with a large blunt median spine. After Osborn.

tion of the *ligamentum nuchæ* and elevator muscles." . . . The importance of such an hypothesis of function will appear in the following description and discussion, and it applies to all the Cetiosauria, namely, to the Morosaurus and Diplodocus types as well, which, so far as known, *are uniform with the camarasaur type in the peculiar bird-like arrangement of the posterior cervicals and anterior dorsals.* (See Fig. 7.)

Again, in the description of Diplodocus, Osborn ('99 (1), p. 200) pointed out the resemblances in the relations of the posterior ribs to those of Apteryx. Two features were brought out, namely: two of the ribs actually underlie the anterior

border of the ilium, both in Diplodocus and Apteryx; the last dorsal vertebra of Diplodocus coalesces with the superior border of the ilium by a bar, which may be considered either a metamorphosed rib or an expansion of the metapophysial lamina: if this is a rib, Diplodocus presents a condition analogous to that in Struthio, in which the last vertebra and rib, technically known as a "pelvic vertebra," is all but united with the ilium. (See Figs. 8 and 9.)

Dorsal Vertebral Formula. — The latest contribution to this subject results from the explorations of 1899 in the dinosaur beds of Wyoming. Holland (1900, p. 817) shows from the explorations of

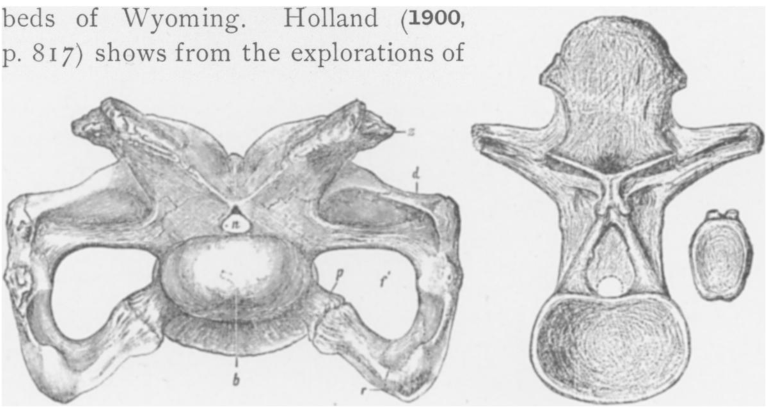


FIG. 7. { Brontosaurus. Posterior cervical, lacking median spine. After Marsh. Camarasaurus. Anterior dorsal vertebra, with blunt median spine. After Cope.

the Carnegie Museum in the Jurassic of Wyoming that the number of dorsal vertebræ in Diplodocus has been overestimated hitherto by Osborn; that this animal possesses in fact only ten dorsal vertebræ, the entire vertebral formula being estimated as follows:

Cervicals	at least	13
Dorsals		10
Sacrals		4
Caudals		32–35

Contemporaneous with this discovery is that of the American Museum party, that the dorsal vertebræ of Morosaurus also number *ten*.

Thus, in two of the largest Cetiosauria or Sauropoda we have an extremely short back, resembling the short back of birds, also an extremely long flexible neck, a very rigid attachment between the sacrum and ilium, correlated with the power of *temporarily raising the entire presacral portion* of the body.

The significance of these avian resemblances in the neck and trunk of these gigantic dinosaurs is rather homoplastic than genetic, for the peculiar paired cervical and cervico-dorsal spines, the posterior abdominal ribs, the lengthened preacetabular iliac bar, correlated with certain feeding motions, are bird-like structures mingled with other non-bird-like structures too numerous to mention. So also with the resemblances among the bipedal dinosaurs, in which the *presacral portion of the body is permanently raised*, bird-like and non-bird-like structures appear in close propinquity.

The main avian character pervading all Dinosauria is the one originally observed by Gegenbaur, namely, the close junction of the astragalus with the tibia or tendency to form a tibiotarsus. However, where there is so much smoke there may be some fire, and we may now proceed to look into the probability of the existence of a primitive bipedal dinosaur-avian ancestor.

V. The Clawed Quadrupedal Ancestry of Birds.

Pycraft ('**96**, p. 261) has recently discussed with care the osteology of Archæopteryx. In opposition to the view of Hurst, that the manus retains five digits, two of which were used in climbing trees, Pycraft supports the older view, that digits I, II, III are the only ones represented, and that digit III, as in the Archosauria[1] generally, and in the Dinosauria in particular, had four phalanges, the terminal of which was armed with a claw. In addition to these reptilian characters are the thecodont, or socketed teeth, the flat, or amphiplatyan,

[1] "Archosauria" is a term employed by Cope for reptiles with two cranial arches at the back of the skull, namely, Rhynchocephalia, Crocodilia, and Dinosauria. In the writer's opinion this group should be extended to include the Lacertilia, in which one arch has been lost.

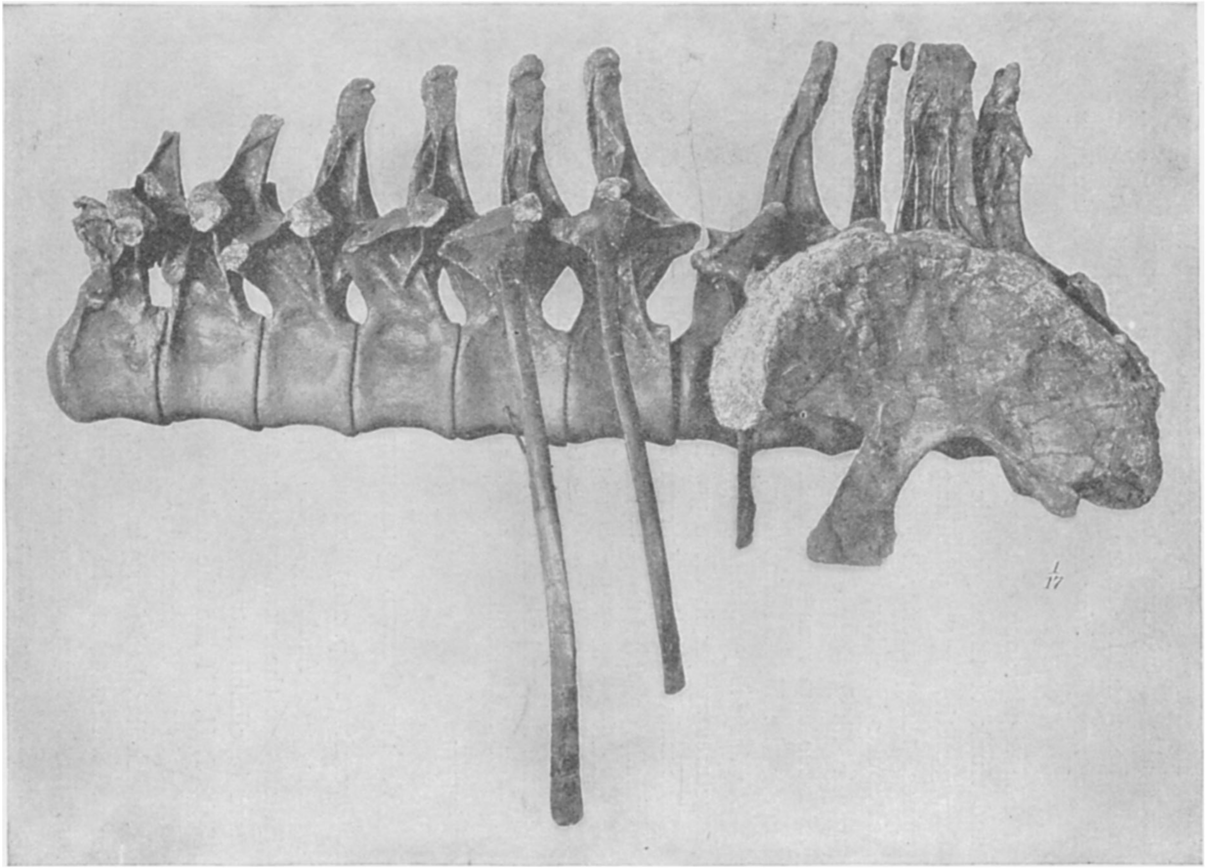


FIG. 8. — Diplodocus. Ninth dorsal vertebra with 9th free rib behind ilium, 10th dorsal, or "pelvic" vertebra, with rib element coalesced with ilium. After Osborn.

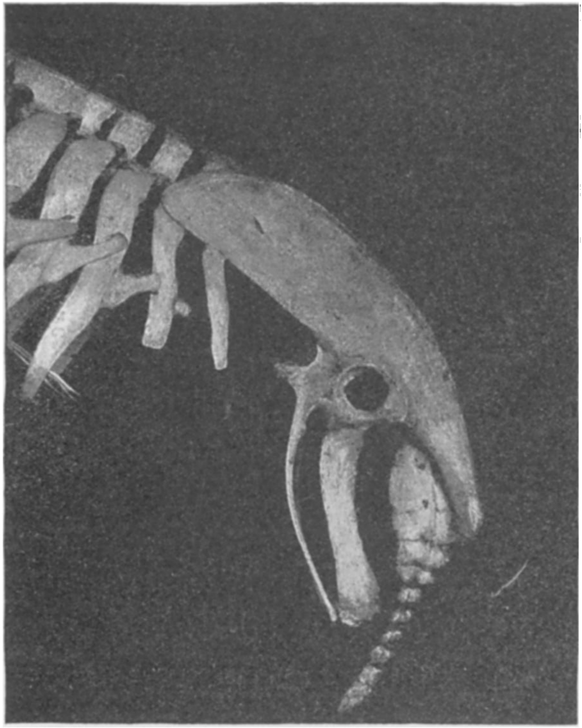
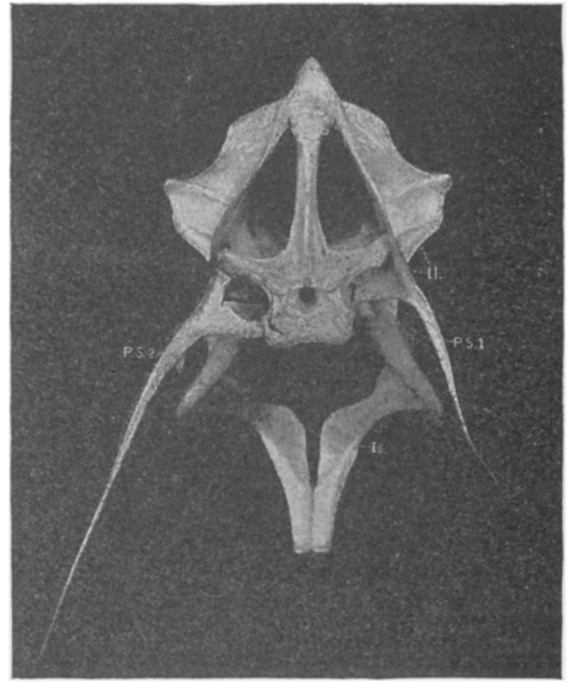


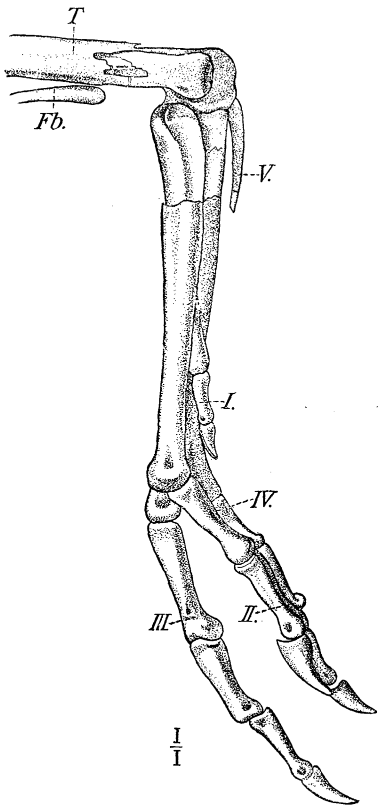
FIG. 9. — Apteryx. Ilium overlapping the two posterior ribs 9th and 10th, as in Diplodocus. Decided *ileo-pectineal* process. Uncinate processes as in Rhynchocephalia.



Struthio. On right side, *P.S.2*, 7th dorsal; on left side, *P.S.1*, 8th dorsal, overlapped by ilium; 9th and 10th dorsals absorbed in sacrum.

vertebral centra, the numerous caudal vertebræ. As regards the ribs, Pycraft considers it unsafe to infer that they lack uncinate processes, since these would be readily macerated off; the cervical ribs were slender and movably articulated. Abdominal ribs appear to have been present, as in the Crocodilia and Proganosauria.

In connection with the clawed quadrupedal stage in the history of birds, Opisthocomus, the H o a c t z i n, proves to be of exceptional interest, "for," as Pycraft remarks, "it is p r o b a b l e



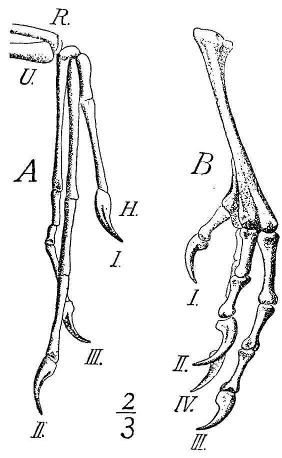


FIG. 10. { Compsognathus. Right pes, × $\frac{1}{1}$. After Baur.
Archæopteryx. *A*, right manus, × $\frac{2}{3}$, from Headley, after Dames; *B*, right pes, × $\frac{2}{3}$, after Owen.
T, tibia; *Fb*, fibula; *R*, radius; *U*, ulna; *I–V*, metacarpals and metatarsals.

that the peculiar habits of the nestling may be a survival of an order of things handed down from the very dawn of avian development." The young are reared in trees and at an early age climb out of the nest; the hand is considerably longer than the forearm; the pollex (I) is especially long and provided with a large claw; index II has an equally large claw, which is

produced beyond the skin fold that encloses the bases of the quills. These proportions are peculiar to the nestlings; the adults shorten the hand and lose the claws as soon as they have ceased to be of assistance; but, as Pycraft observes, could we discover a yet more primitive form "it is probable we should find that the claws and long hand were maintained throughout life." Further light upon the quadrupedal habits of primitive birds is given by the very interesting observation of Dean upon the locomotion of young cormorants, which, when frightened, clamber over irregular surfaces with the assistance of the fore limbs. Young gallinules, coots, and grebes are also quadrupedal in habit.

So far, therefore, as the osteology of Archæopteryx and the embryology and habits of recent birds guide us, the theory of a quadrupedal proganosaurian prototype is not excluded.

VI. The Most Primitive Quadrupedal Land Reptiles.

This suggests a consideration of the Proganosauria, the most primitive representatives of the Hatteria phylum, as one of the possible sources of the birds.

The Proganosauria, Baur (= Proterosauria, Seeley), constitute a suborder of Rhynchocephalia and include some of the most ancient reptiles known of the Permian period. They occupy the cleft between Crocodilia, Lacertilia, and Dinosauria.

In his extremely interesting and important papers upon Palæohatteria and Kadaliosaurus Professor Hermann Credner (**'88, '89**) has described two proganosaur types from the Permian, near Dresden, one of which approaches most nearly the hypothetical ancestral dinosaur. Palæohatteria, if we may judge by the comparatively unossified extremities of the limb bones, was probably an aquatic type; Kadaliosaurus, on the other hand, was undoubtedly a land type, the limb bones being completely ossified proximally and distally, with spongy interior. The prefix *καδαλίων* refers to the exceptional elongation of the limbs, the proportions of which are well represented in Fig. 11. Professor Credner has pointed out the striking resemblance of the somewhat forward and backward spreading ilium

of this animal to that of a dinosaur. It is further to be noted that, while the forearm is extremely long, the metacarpals are shorter than the metatarsals, which are decidedly long and slender; the skull and shoulder girdle are unfortunately unknown; the number of dorsals is estimated at twenty; there are two sacrals. While the ectepicondylar foramen of the humerus points in the direction of the lizards (in distinction from Palæohatteria, with its entepicondylar foramen), there is no

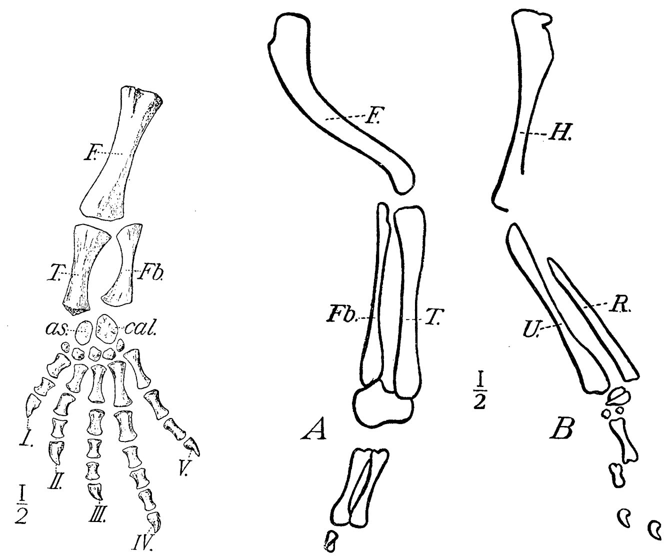


FIG. 11.—Limbs of Proganosauria.

Palæohatteria. A short-limbed, probably amphibious type. Left hind limb. Restored by McGregor, after Credner.

Kadaliosaurus. A long-limbed, probably terrestrial and active type. Metatarsals longer than metacarpals. After Credner.

question that we have here a type which comes very near the dinosaur atavus. The fact that the humerus and femur are of the same length accords with the condition characteristic of the early Cetiosauria, for the Cetiosaurus of Oxford has a humerus and femur of nearly equal length.

The foot structure of Palæohatteria, as restored from Credner's plates by Dr. McGregor (Fig. 11), fulfills all the required ancestral conditions, both for dinosaurian and avian ancestry.

Granting, therefore, for the sake of argument, the hypothetical value of the Proganosauria in the largest sense as

ancestral to all Archosauria, including birds, the crucial question remains, whether birds sprang off independently from a proganosaur stem or from a common dinosaur-avian stem. In the origin of the birds we have to imagine, first, a terrestrial stage, in which bipedal was gradually substituted for quadrupedal progression ; it would appear probable that the bipedal progression was first acquired during a terrestrial stage, because the foot of birds is primarily a walking, and not a climbing, organ ; second, a cursorial bipedal or, more probably, an arboreal stage, in which both fore limb and tail enjoyed a change of function contemporaneous with the acquisition of feathers.

VII. Correlated Development of Tridactylism and Bipedal Progression.

It appears probable that the ancestral dinosaur was a quadrupedal type, with the body well raised off the ground, distinctively a land animal, because the distinctive specialization of this group appears to have been terrestrial, the Cetiosauria or Sauropoda secondarily acquiring an amphibious mode of life. The manner in which the four-footed primitive dinosaurs acquired the bipedal habit and consequent reduction of the fore limbs and elongation of the hind limbs is beautifully illustrated in Chlamydosaurus of Australia and some other living lizards. As observed by Saville-Kent, this animal in all its rapid movements raises the fore limbs, balances the anterior part of the body with the tail, and runs along rapidly upon the hind limbs. This analogy appears to demonstrate that an important function of the tail was to serve as a balancing organ. (We note in parenthesis that this function is developed among birds.) Kent remarks further : "Such is the construction of the hind foot and its component digits that, when thus running, the central digits only, rest upon the ground. As a consequence of this structural peculiarity, the track made by this lizard when passing erect over damp sand or other impressible soil would be tridactyl, like that of a bird, and would also correspond with the tracks that are left in Mesozoic strata by various typical Dinosauria. This tridigitigrade formula of the

gradation of Chlamydosaurus, induced by the great relative shortness of the first and fifth digits, is distinctly indicated in Fig. 1 of the plate previously referred to."

Thus, tridactylism is correlated with rapid bipedal progression, the inner and outer digits suffering reduction. In fact, a glance at the digital formula of Archosauria shows why tridactylism is a likely resultant of rapid digitigrade progression.

Digits . . .	I	II	III	IV	V
Number	1	1	1	1	1
of	2	2	2	2	2
Phalanges		3	3	3	3
in			4	4	
Archosauria				5	

There is considerable ground for regarding a certain degree of bipedalism as a character common to all dinosaurs. Among the carnivorous Megalosauria there can of course be no question, because this condition marks the oldest Triassic types. Osborn, in Diplodocus, has demonstrated the truth of Cope's conjecture that the quadrupedal cetiosaurs occasionally rose upon their hind limbs. Among the Predentata, the Iguanodontia are typically bipedal, and the iguanodont or quadriradiate structure of the pelvis in the quadrupedal Stegosauria and Ceratopsia has led Dollo to advance the somewhat daring hypothesis that these animals also were at one stage more or less bipedal and that their fixed quadrupedal habit is possibly secondary.

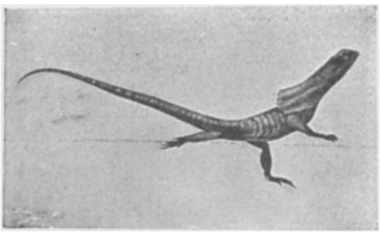


FIG. 12. — Chlamydosaurus in rapid motion. From an instantaneous photograph by Saville-Kent.

VIII. Hypothetical Origin of Birds from a Primitive Bipedal Dinosaur.

If bipedalism subsequently proves to be a common dinosaur character, it would naturally strengthen the dinosaur-avian stem hypothesis. The presence of a *free quadrate* in birds, a

difficulty which suggested itself to Marsh, is explainable as a secondary character, like the secondarily free quadrate of certain Lacertilia and Ophidia, due to degeneration of one of the cranial arches.

The passage from a quadrupedal to a bipedal type would also mark the transition from the Proganosauria to the Dinosauria, and all that our present knowledge and evidence justify us in saying is that *in this bipedal transition, with its tendency to form the tibiotarsus, the avian phylum may have been given off from the dinosaurian.*

This form of the Huxleyan hypothesis seems more probable than that the avian phylum should have originated quite independently from a quadrupedal proganosaur, because the numerous parallels and resemblances in dinosaur and bird structure, while quite independently evolved, could thus be traced back to a potentially similar inheritance.

Upon the whole, therefore, the dinosaur-avian stem hypothesis deserves not to be discarded but to be very seriously reconsidered in connection with future research and discoveries among birds and dinosaurs.

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